

MATING BEHAVIOR AND SPAWNING IN TWO NEUSTONIC NUDIBRANCHS IN THE FAMILY GLAUCIDAE

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ABSTRACT

We observed the mating behavior and egg production rates of *Glaucus atlanticus* (Forster, 1777) and *Glaucilla marginata* (Bergh, 1868), neustonic nudibranchs of the family Glaucidae, collected from the western Pacific Ocean near Australia. Although the same sequence of mating behaviors occurred in both species, the timing of these behaviors and mating duration were different. The entire mating sequence from "kiss" to separation lasted about one hour in *G. atlanticus* and about one minute in *G. marginata*. Morphological differences that could be associated with this difference are discussed. Glaucids release short gelatinous strings of eggs at varying frequencies. Egg production rates in both species were directly related to food availability, though both species continued to produce eggs at lower rates for several days with little or no food. Both glaucids exhibited several characteristics of planktotrophic development: eggs were small (70 μm by 80 μm), embryonic developmental times were short (2.5 to 3.0 days at 19°C), and veligers swam longer than a week.

Only a small number of nudibranchs spend their entire life in the water column, and these species have few evolutionary adaptations to pelagic life. Several characteristics, such as no heavy shell and some swimming ability, that could be considered advantages in a pelagic habitat are also found in benthic nudibranchs. Some pelagic nudibranchs are flattened or otherwise modified and do not resemble benthic nudibranchs, but two species of Glaucidae, *Glaucus atlanticus* (Forster, 1777) and *Glaucilla marginata* (Bergh, 1868), are easily identified as eolid nudibranchs by their cerata. Like other nudibranchs, the Glaucidae are reciprocal hermaphrodites, although little is known about their mating behavior and spawning characteristics (Lalli and Gilmer, 1989).

Both glaucids are neustonic, occurring in the surface layer of tropical oceans. *Glaucus atlanticus* is circumtropical. *Glaucilla marginata* is restricted to the tropical Pacific Ocean. Both species float upside down on the air-seawater interface and neither is a good swimmer. Their distribution is primarily controlled by winds, as is also true of their cnidarian prey, *Physalia*, *Vevela*, and *Porpita* (Lalli and Gilmer, 1989). Like other neustonic animals, they are countershaded, blue to purple on their ventral surface which faces up, and white or silvery on their dorsal side facing down. Thompson and Bennett (1970) discovered that *G. atlanticus* stores nematocysts derived from their prey in cnidosacs at the tips of the cerata. The

utilization of nematocysts as a defense against predators is well known in eolid nudibranchs, although the processes involved in the control of the discharge of these nematocysts are not well understood (Todd, 1981; Thompson and Bennett, 1970).

There are several differences between *Glaucus atlanticus* and *Glaucilla marginata* that are important to a discussion of their mating behavior (Lalli and Gilmer, 1989). *G. atlanticus* is the larger of the two species, reaching a maximum reported length of 43 mm (Miller, 1974). It has a long slender foot, and a long, strong, contractile penis armed with a chitinous spine. The long cerata are arranged in single rows in three to four clusters projecting from lobes on the sides of the body. The central ceras is much longer than those on the sides of the cluster. A single individual can have up to 85 cerata. *G. marginata* is smaller than *G. atlanticus*, with previous recorded sizes up to 12 mm, and up to 18 mm in this study. The penis is not armed and the cerata are arranged in multiple layers in four clusters. *G. marginata* can have twice as many cerata as *G. atlanticus*. In both species the reproductive aperture is just posterior and level with the bottom of the first right ceratal arch.

Despite their widespread distribution, observations and experiments on live *Glaucus atlanticus* and *Glaucilla marginata* are rare, perhaps because they are usually damaged when

when they are collected with nets. In this paper we will compare the pattern and timing of mating behavior in these two pelagic nudibranchs. We will also describe and quantify spawning and egg production in both species, and the effect of starvation on egg production in *G. marginata*. Some observations of the egg ribbons and embryonic developmental times will be described. However, veligers did not complete metamorphosis to adult in our laboratory.

METHODOLOGY

COLLECTION AND MAINTENANCE OF ANIMALS

We found glaucid nudibranchs in the surf zone and blown onto the beaches of New South Wales, Australia, south of Sydney, in the austral summer of 1979-1980. *Glaucus atlanticus* were collected in early December from Morulga and Bawley Beaches, and *Glaucus marginata* were collected in early December from North Kioloa Beach, and early March from South Kioloa Beach. No glaucids were found on a search of the sand and surf zones of a group of beaches in this area from mid-December until late February. The beaches were regularly inspected by the manager of the Kioloa Field Station of the Australian National University (ANU). Surf zone temperatures were 20.5°C on 11-12 December, and 22.0°C on 2 March. We scooped glaucids from the surf into containers of seawater and returned them to the laboratory at ANU.

At ANU, adult glaucids were kept in three 10.0 l rectangular seawater aquaria (two per aquarium) at room temperature (about 20°C) or at 19°C in shallow 1.0 l plastic boxes. Seawater in the containers was changed two to three times a week. Both glaucids were fed either fish food or pieces of *Physalia* sp. collected from the same beaches and frozen until use.

MATING BEHAVIOR

We observed the sequence and timing of mating behavior for three pairs of *Glaucus atlanticus* and six pairs of *Glaucilla marginata*. Mating behavior was observed and timed either in the aquaria or in large shallow containers.

SPAWNING BEHAVIOR AND EGG PRODUCTION RATES

Glaucids release strings of eggs, and do not lay down an egg mass like other eolid nudibranchs. Dimensions of egg capsules from seven strings released by *Glaucus atlanticus* were measured using a compound microscope with a calibrated micrometer. In addition, we measured the lengths of 20 strings and the number of eggs in each string for strings released four days after collection. Time intervals between release of strings were recorded for five individuals in order to calculate daily fecundities. Fresh spermatozoa were also measured using a compound microscope. For *Glaucilla marginata*, egg capsule size was measured in 11 strings released by adults collected in March.

Ten *Glaucilla marginata* collected in March were used to evaluate the response of egg production rate to a decrease in food availability. Each adult was isolated immediately after

collection, and removed from the jar and placed in fresh seawater at 12, 24 and 36 hr after collection. All the strings and the number of embryos per string in at least 15 strings were counted for each individual for each of the three 12 hr periods. The length of the string was also measured for the first 12 hr period. At the end of 36 hr, the total length and wet weight in grams of each individual were measured. We estimated the egg production rate for freshly collected animals and for animals kept without food for periods up to 36 hr.

DEVELOPMENT

Some egg strings were maintained in aerated glass jars at 19°C to determine embryonic developmental times, and to observe survival and behavior of the larvae after hatching. The age of the strings was known to within 12 hr. Embryos of both glaucids hatched. Veligers were inspected for continued survival and swimming ability until they sank to the bottom of the jars and died.

RESULTS

MATING BEHAVIOR

Mating in both *Glaucus atlanticus* and *Glaucilla marginata* involved a sequence of predictable and stereotypic behaviors. These behaviors were the same for both species and began when conspecific glaucids contacted each other. Although there was some variation in the exact timing of each behavior type in the sequence, total duration of mating was similar for all pairs of the same species.

The first in the sequence of behaviors was the relatively brief "kiss". Partners oriented so that their mouths and ventral surfaces were touching, and the heads usually submerged. Shortly after the mouths joined, the penises emerged. The penises were greatly extended, and sometimes the end of one penis was wrapped around the other individual. The second major behavior was the intertwining of the two penises, and the two individuals began to couple. Initially the mouths separated, but the pair were still oriented ventral surface to ventral surface (Fig. 1a). Both glaucids arched the body and the cerata clusters toward their dorsal surfaces, keeping the cerata away from each other. During mating we observed individuals flinch and arch away when touched by the cerata of the mate. This observation indicated that a ceras could be stimulated by this contact to eject the cnidophages in the cnidosacs at the tip of the ceras, and the partner could be stung by the nematocysts from the cnidophage. Shortly after coupling began, the pair changed to a side by side orientation with the ventral surfaces on the air-water interface and the penises lying between the two parallel bodies (Fig. 1b). During coupling the pair could be either head to head or head to tail, and often switched from one to the other once or twice during this time period. The pair lay quietly between changes in orientation. Penises were loosely intertwined until two-thirds through the coupling period when the penises became tightly intertwined (Fig. 1c). When the pair began to separate, the coil untwisted, the penises showed some thickening as they started to retract, and the nudibranchs flexed their bodies (Fig. 1d). Total retraction of the penises required a much longer



Fig. 1. *Glaucus atlanticus*. Sequence of mating behaviors: (a) 7 min after initial contact, ventral surface to ventral surface; (b) 37 min after initial contact, coupled, penises in loose coil, ventral surfaces at the air/water interface; (c) 47 min after initial contact, coupled, penises in tight coil; (d) 58 min after initial contact, separated, penises beginning to retract, note thickening. Horizontal field width = 40 mm.

period of time than separation of the two individuals.

Although the pattern of behavior for the two species of glaucids was identical, the timing of each behavior and the duration of mating was very different. For *Glaucus atlanticus*, the "kiss" lasted about four min. Between four and nine min into the sequence the pair reoriented so they were parallel, usually head to tail, with the penises loosely coiled between them. The coil tightened 36 to 41 min into the sequence, remained tight for four to nine min, then loosened again. Separation took four to nine min and was complete 43 to 59 min after the initial joining. Retraction of the penis took up to an hour (19, 52 and 61 min).

For *Glaucilla marginata*, the mating sequence was substantially shorter. The "kiss" lasted five sec. Pairs then twisted, and oriented parallel to each other with their ventral surfaces facing up and penises twisted around each other. Coupling lasted 60 sec (range 50 to 70 sec, SD = 8.4 sec). Separation was fast, and the penises retracted quickly, within 21 sec (range 10 to 35 sec, SD = 8.6 sec). The total time for mating was 65 sec, about 2% of the time taken by *Glaucus atlanticus*.

The ability to mate again with the same or a different individual immediately after mating was investigated in both species. A pair did not remate after retraction of the penises, even if they were pushed together. But we observed that a

third non-mated glaucid will extrude its penis in the presence of a mating pair. In *Glaucilla marginata* we saw these new individuals mating with recently mated glaucids.

SPAWNING AND EGG PRODUCTION

Both species released their eggs in straight strings about 0.3 mm in diameter that sank slowly (about 50 m d⁻¹). Strings were from 5.0 to 17.5 mm long for *Glaucus atlanticus*, and from 2.0 to 6.4 mm for *Glaucilla marginata*. In both species ova were individually encapsulated (primary membrane). Egg capsules were oval, and evenly spaced slightly less than one diameter apart within the egg string. A thin transparent tube (secondary membrane) surrounded the egg capsules within the mucous string (Fig. 2). Egg capsules of the two glaucids were similar in size: *G. atlanticus*, 60 to 75 μm wide and 75 to 97 μm long; and *G. marginata*, 58 to 67 μm wide and 74 to 82 μm long. Sperm of *G. atlanticus* were long and slender (129 μm by 0.9 μm).

Daily or hourly fecundity was a function of the number of embryos in a string, and the rate of string production. The number of eggs per string was a linear function of the length of the string, but smaller *Glaucilla marginata* released strings that were less than half the length and contained less than half the embryos of those released by *Glaucus atlanticus* (Fig. 3). The time interval between strings was also different for

the two species. Even after three to four days in the laboratory *G. atlanticus* produced 4-6 strings/hr (average for five individuals was 3.8 strings/hr). *G. marginata* released 8.6 strings/hr during the first 12 hr after collection, twice the frequency of *G. atlanticus*. However, the frequency dropped to less than two strings an hour during the next 12 hr. Since the number of embryos per string ranged from 36 to 96, *G. atlanticus* released from 3300 to 8900 embryos/day, even after three to four days in the laboratory. The fecundity for freshly collected *G. atlanticus* was about the same, from 1850 to 9250 embryos/day.

The relationship between size and egg production and the effect of starvation on egg production was quantified for *Glaucilla marginata*. First, although total length (TL) and wet weight of the ten individuals measured were significantly correlated, egg production (EP in number/hr) was more closely related to total length ($EP = 597.2 TL - 571.2$, $r^2 = 0.56$) (Fig. 4) than to wet weight ($r^2 = 0.27$). The increase in egg production with increasing size was a function of both increased string production (strings/hr, $r_s = 0.705$) and closer packing of egg capsules in a string (eggs per string, $r_s = 0.675$), but not an increase in the length of the string with total length of the glaucid ($r_s = 0.421$, ns) (Spearman's rank correlation coefficient, $p = 0.05$; Siegel, 1956). The total length of *G. marginata* ranged from 12.6 to 17.9 mm, string production ranged from 3.3 to 12.9 strings/hr, and the average number of eggs per string ranged from 25.5 to 41.7 ($n = 15$ strings per individual). The average string length of the same 15 strings ranged from 3.8 to 5.1 mm, with 95% confidence intervals of 0.2 to 0.5 mm. Differences in average string length between individuals was not a significant factor in the increase in egg production with size.

Egg production rates of starved *Glaucilla marginata* decreased significantly after 12 hours ($X^2 = 15.2$, Friedman two-way ANOVA, $p > 0.001$; Siegel, 1956), but then remained the same during the remainder of the experiment (Fig. 5). Egg production rates in the first 12 hr after collection were 3.5 times rates in the second and third 12 hr intervals after collection,

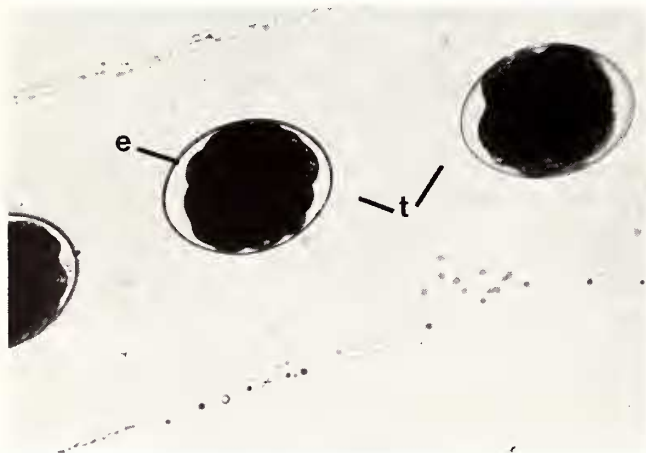


Fig. 2. *Glaucus atlanticus*. Development at 19°C; embryos about 24 hours after release, multiple cell stage [e, egg capsule (primary membrane); t, internal tube (secondary membrane)]. Horizontal field width = 300 μ m.

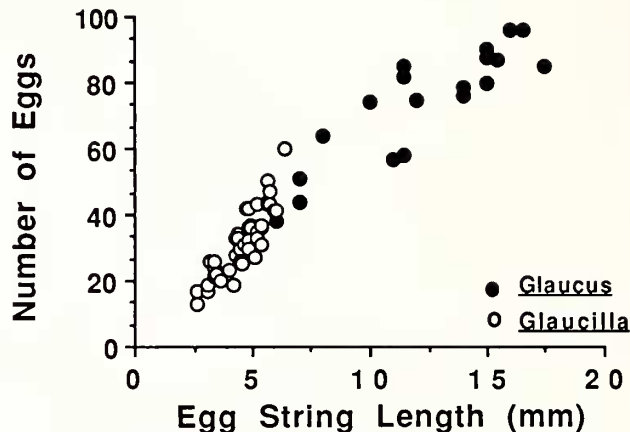


Fig. 3. Relationship between egg string length and the number of eggs per string for *Glaucus atlanticus* (\bullet = one pair) and *Glaucilla marginata* (\circ = 4 individuals).

which were the same ($U = 43$, Mann Whitney U, $p = 0.05$, Siegel, 1956). *G. marginata* was still producing eggs after 36 hr with no food.

Lower egg production rates in starved *Glaucilla marginata* were due to fewer strings produced/hr and fewer egg capsules per string. String production decreased to 36 to 39% of initial rates, and egg capsules per string to 59 to 71% of initial values. Although the decrease in egg capsules per string could be due to shorter strings or to greater spacing between the egg capsules or both, four of the ten *G. marginata* produced some very short strings with only one or two eggs per string during the second and third 12 hr periods of starvation. Thus string length could decrease during starvation.

DEVELOPMENT

Embryos of *Glaucus atlanticus* began to divide after a few hours at 19°C. At about 24 hr, the embryos were multicellular. The egg capsules were still separated within the string, but the secondary membrane was thinner and constricted between the embryos (Fig. 2). Between 48 and 60 hr, embryos had beating cilia (trochophore), and the secondary membrane began to disintegrate. After about three days at 19°C, the half-shelled veligers moved slowly through the mucous string and swam away. The shell was initially ovoid but became coiled after a few days. Starved veligers of *G. atlanticus* swam continuously for seven to 11 days after hatching before sinking to the bottom of the containers, and dying before metamorphosis into juveniles. The shell was 89 μ m by 104 μ m, larger than the egg capsule. Embryonic developmental time for *Glaucilla marginata* was about the same, 2.5 to 3.0 days at 19°C. These embryonic developmental times were slightly slower than found for *G. atlanticus* veligers maintained at 25°C (2.0 days, Bebbington, 1986). The bilobed veligers of *G. marginata* swam continuously for 33 days after hatching before they died without metamorphosing. The shell was 96 μ m by 119 μ m.

Thus both species showed characteristics of planktonic development: small eggs, short embryonic

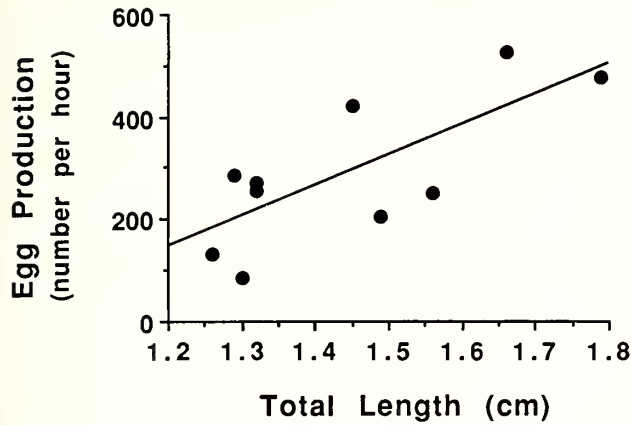


Fig. 4. *Glaucilla marginata*. Relationship between animal size, total length, and egg production 12 hr after collection.

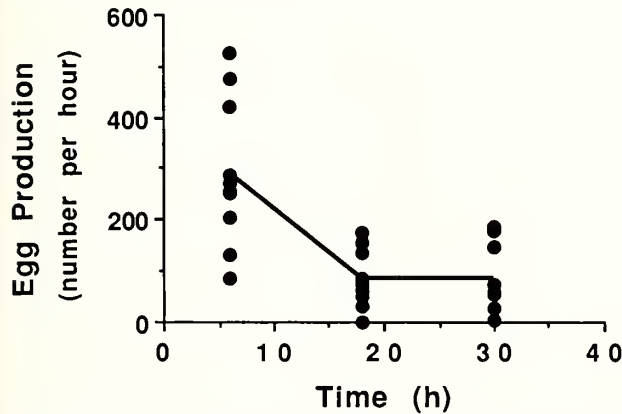


Fig. 5. *Glaucilla marginata*. Decrease in egg production over time with no food available. Points are average egg production rates for three 12 hr intervals after collection for 10 individuals.

developmental times, and veligers that spend several weeks swimming in the plankton. Veligers of *Glaucus marginata* survived three times longer in the laboratory than did veligers of *Glaucus atlanticus*, but the veligers of *G. marginata* were given a mixture of marine phytoplankton which could have increased their survival times. We were unable to stimulate metamorphosis, but are unsure whether the inability of the veligers to metamorphose was due to inadequate diets or lack of the appropriate substrate as is necessary for most eolid nudibranchs (Harrigan and Alkon, 1978; Thompson and Brown, 1984).

DISCUSSION

Glaucus atlanticus found on the beaches of New South Wales in Australia were of the typical color pattern and within the size range found elsewhere in the world (Bennett, 1836; Bieri, 1966; Miller, 1974; Thompson and McFarlane, 1967). *Glaucilla marginata* have been recorded only once before from Australian waters (Thompson and Bennett, 1970). *G. marginata* collected in this study were 18 mm in length, much larger than previously reported (Thompson and Bennett, 1970), and the ventral surface was not brown but deep purple - similar to *G.*

atlanticus. Differences in coloration could be due to differences in diet between the two groups of *G. marginata*, as found for other pelagic nudibranchs (Lalli and Gilmer, 1989). We never found the two species of glaucids together, but both species were always found with some of their cnidarian prey.

Previous reports of mating behavior are sparse for *Glaucus atlanticus* and nonexistent for *Glaucilla marginata* (Lalli and Gilmer, 1989). Possibly because he did not observe the complete stereotypic mating sequence of *G. atlanticus*, Bebbington (1986) stated that *G. atlanticus* paired laterally or ventrally during copulation in the laboratory. We found that *G. atlanticus* pairs both laterally and ventrally, but at different times during the same mating sequence.

Mating in *Glaucus atlanticus* was exceptionally long compared to other pelagic nudibranchs, whereas mating duration in *Glaucilla marginata* was similar to other species of pelagic nudibranchs, one to fifteen minutes (Lalli and Gilmer, 1989). Maximizing the reproductive potential of each encounter may be particularly important to a pelagic species that must depend on chance encounters to find a mate. In the pelagic realm there are several options for exchanging large amounts of sperm: an exchange of spermatophores as found in heteropods and thecosomes; prolonged mating as found in gymnosomes and *G. atlanticus*; mating with many partners sequentially in swarms or rafts as is true of one species of pelagic dendronotacean (Lalli and Gilmer, 1988).

For the neustonic glaucids, wave and wind action at the surface make prolonged mating difficult. First, wave action will tend to separate partners. Second, both glaucids utilize nematocysts (Lalli and Gilmer, 1989). Contact with a mate could stimulate the contraction of the muscle complex around the cnidosac and the release of the cnidophage and nematocysts into the water, thus stinging the partner. In eolid nudibranchs, the nematocysts are in cnidophage cells inside the cnidosac. When the muscles surrounding the cnidosac contract, the cnidophage is ejected through the cnidopore or the epithelium at the tip of the ceras. If the cnidophage membrane ruptures on release, the nematocysts usually discharge (Greenwood and Mariscal, 1984). Stimulation of special neurosensory cilia which are concentrated at the ceras tip could cause contraction of the cnidosac wall (Todd, 1981). Mere pinching of the ceras with metal forceps (Thompson, 1976) or pressure on a cover slip (Greenwood and Mariscal, 1984) will stimulate ejection of cnidophage cells in many eolids. Both glaucid species actively avoid each other's ceras, and individuals flinch when touched by the cerata of their partner during mating. For benthic eolid nudibranchs neither problem occurs. Wave action is minimal, and the cerata tips are oriented dorsally not to the side as is true of the glaucids.

Morphological adaptations in *Glaucus atlanticus* appear to have solved both of these difficulties. The chitinous spine on the penis of *G. atlanticus* may help prolong contact in the face of wave action, and thus may be a singularly important morphological adaptation to long mating times (Miller, 1974). In contrast, pelagic nudibranchs with shorter mating times have unarmed penises. In addition, in *G. atlanticus* the cerata are fewer, longer and in a single layer, so are more easily held away from the partner than in *Glaucilla marginata*.

Prolonged copulation may mean more sperm are exchanged, filling the seminal receptacle. If prey are available, fertile egg production can continue longer before finding another mate is necessary. This could be advantageous when finding a mate depends primarily on physical forces in the ocean and not active searching. With the exception of *G. marginata*, the other species of pelagic nudibranchs are more active swimmers, and/or mate in swarms or cling to a surface flotsam (Lalli and Gilmer, 1989), so finding a mate is not as dependent upon physical forces in the ocean.

Our observations of the frequency of egg string production and of the number of eggs per string for *Glaucus atlanticus* were different from those of Bebbington (1986) and Macnae (1954). Although Bebbington saw fewer ova per string, strings were produced much more frequently, leading to fecundity estimates about six times ours. Bebbington gives no information about how long his glaucids were kept in the laboratory or their feeding conditions. Macnae (1954) also found fewer ova per string and greater spacing between embryos than we did, but did not estimate frequency of string production. We observed that egg production in *G. atlanticus* increased within hours of ingesting a slurry of homogenized *Physalia*. There was no interval between strings, instead of the 10 to 15 min interval between strings found when this species was fed fish food. These combined observations on egg production in *G. atlanticus* in conjunction with the results of the experiment on the effect of starvation on egg production in *Glaucilla marginata* suggest that egg production in glaucids may be closely coupled to their recent feeding history. Thus the inter- and intraspecific differences in rates of egg production observed for the two glaucids may be due to differences in their immediate nutritional histories.

There appear to be no major adaptative differences in reproduction and development between these neustonic eolids and their benthic relatives. Egg strings have the same basic form (hollow, cylindrical, capsule-filled cord) as benthic eolids, but the ribbon floats free as a short uncoiled string of eggs such as found in other pelagic nudibranchs instead of being attached on one side (Lalli and Gilmer, 1989). Many other species have only one ova per capsule (Hurst, 1967). The presence of a secondary membrane is not common, but its function is unknown (Eyster, 1986). Glaucids have relatively high fecundities compared to benthic eolid nudibranchs of the same size range (Harris, 1975; Rivest, 1978) and compared to the only other pelagic nudibranch, *Phylliroe bucephala* (Peron and Lesueur, 1810), for which we have fecundity estimates (Lalli and Gilmer, 1989). High fecundities and a direct linkage of egg production to food availability are valuable characteristics for these neustonic glaucids which have an unpredictable food source that occurs in large quantities.

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